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RESEARCH PAPER

Biotic interactions mediate patterns of herbivore diversity in the Arctic

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ABSTRACT

Aim Understanding the forces shaping biodiversity patterns, particularly for groups of organisms with key functional roles, will help predict the responses of ecosystems to environmental changes. Our aim was to evaluate the relative role of different drivers in shaping the diversity patterns of vertebrate herbivores, a group of organisms exerting a strong trophic influence in terrestrial Arctic ecosystems. This biome, traditionally perceived as homogeneous and low in biodiversity, includes wide variation in biotic and physical conditions and is currently undergoing major environmental change.

Location The Arctic (including the High Arctic, Low Arctic and Subarctic)

Methods We compiled available data on vertebrate (birds and mammals) herbivore distribution at a pan-Arctic scale, and used eight variables that represent the most relevant hypotheses for explaining patterns of species richness. We used range maps rasterized on a 100 km × 100 km equal-area grid to analyse richness patterns of all vertebrate herbivore species combined, and birds and mammalian herbivores separately.

Results Overall, patterns of herbivore species richness in the Arctic were positively related to plant productivity (measured using the normalized difference vegetation index) and to the species richness of predators. Greater species richness of herbivores was also linked to areas with a higher mean annual temperature. Species richness of avian and mammalian herbivores were related to the distance from the coast, with the highest avian richness in coastal areas and mammalian richness peaking further inland.

Main conclusions Herbivore richness in the Arctic is most strongly linked to primary productivity and the species richness of predators. Our results suggest that biotic interactions, with either higher or lower trophic levels or both, can drive patterns of species richness at a biome-wide scale. Rapid ongoing environmental changes in the Arctic are likely to affect herbivore diversity through impacts on both primary productivity and changes in predator communities via range expansion of predators from lower latitudes.

Keywords

Biodiversity, biotic interactions, predator–prey, species richness, trophic interactions, tundra.

INTRODUCTION

Biodiversity plays a key role in maintaining the stability of ecosystems facing anthropogenic environmental changes (Hautier *et al.*, 2015). In addition to the role of evolutionary processes and species dispersal, current biodiversity patterns are strongly determined by environmental constraints. Understanding what shapes patterns of biodiversity, particularly for groups of organisms with key functional roles in ecosystems, will improve predictions about the responses of ecosystems to ongoing environmental changes. Despite recent attempts to document biodiversity and to anticipate the effects of rapid and unprecedented change in the Arctic (e.g. CAFF, 2013), analyses of diversity patterns, and especially of their drivers, are still lacking for this region. Given the relative simplicity of Arctic food webs and the extreme abiotic conditions, the Arctic has been proposed as a model for understanding the interactions between biotic and abiotic elements in ecosystem functioning. Furthermore, as a temperature-limited system that is rapidly warming due to climate change, the Arctic may be regarded as a bellwether for the changes to come in other systems (Post *et al.*, 2009).

Herbivores have a pervasive effect on the structure and dynamics of tundra ecosystems (Bråthen *et al.*, 2007; Olofsson *et al.*, 2012) and can moderate the effects of climate change on plant growth (Olofsson *et al.*, 2009). The composition of herbivore communities may play a crucial role in determining the impacts of herbivory on the structure and dynamics of ecosystems (Ritchie & Olff, 1999) and their associated processes (Metcalfe & Olofsson, 2015). Understanding how the diversity of herbivores varies across the Arctic can help disentangle the various outcomes of plant–herbivore interactions in the tundra; something of great importance given the scope and pace of change occurring in the Arctic.

The mechanisms behind large-scale patterns of biodiversity have been discussed by ecologists for decades, and several non-exclusive hypotheses have been proposed with different levels of empirical support (Table 1). However, the relative importance of the underlying processes may differ between specific guilds (Kissling *et al.*, 2012) and drivers of herbivore diversity have not been extensively investigated (but see Olff *et al.*, 2002, for temperate and tropical areas). Here, we test eight explanatory variables (with their underlying hypotheses; see Table 1) to explain large-scale geographical patterns of herbivore species richness in the Arctic. In global analyses, one of the most supported hypotheses is the 'species–energy' hypothesis (Wright, 1983; Currie, 1991), which states that higher energy availability, either through the amount of energy entering the system (ambient energy, H1a) or through productivity (productive energy, H1b), allows more species to coexist. Broad patterns of species diversity in the Arctic, with decreasing species richness with increasing latitude, have been related to decreases in primary productivity associated with lower temperatures at higher latitudes (Legagneux *et al.*, 2014). However, the relative influence of ambient versus productive energy as a driver of diversity of Arctic species has not been evaluated.

Other important drivers of species richness include environmental heterogeneity, which increases the number of available niches for different species to coexist and interact. Typically, two different (but potentially related) aspects of environmental heterogeneity have been measured: the number of habitat types (i.e. habitat heterogeneity, H2a; Kerr *et al.*, 2001) and the range in elevation (i.e. topographic heterogeneity, H2b; Kerr & Packer, 1997) in an area. Topographic heterogeneity has often been used as a surrogate for microclimatic conditions in broad-scale studies (Sandom *et al.*, 2013); it seems to be a strong driver of mammal species richness at lower latitudes (Davies *et al.*, 2007) and may also increase local diversity of terrestrial vertebrates in the Arctic (CAFF, 2013).

Other potential drivers of broad-scale patterns of species richness relate to historical and geographical influences, edaphic factors and biotic interactions (Field *et al.*, 2009). In the Arctic, historical and geographical drivers, such as limitation of colonization and evolutionary effects, are likely to play a major role in patterns of species richness (Davies *et al.*, 2011). Climatic oscillations in the Quaternary affected phylogeographical patterns of some Arctic species (Waltari & Cook, 2005) and have influenced present-day patterns of diversity (Davies *et al.*, 2011). The extent of ice cover since the Last Glacial Maximum (LGM) about 21,000 years ago (H3) has influenced current patterns of overall diversity (Hawkins *et al.*, 2003b) and the colonization of particular Arctic regions (Normand *et al.*, 2013). Some areas, like Beringia, acted as climatic refugia during the Quaternary and currently host the highest animal and plant diversity in the Arctic. Similarly, geographical position relative to the coastline (H4) can have an influence on the distribution of terrestrial vertebrate herbivores in the Arctic, where coastal zones provide important habitats for some herbivores (e.g. Ward *et al.*, 2005) but also subsidize their predators (Oksanen *et al.*, 2013). For example, populations of small mammalian herbivores in coastal areas can be controlled by jaegers (*Stercorarius* spp.), whose populations can alternatively subsist on fish and other marine food sources (Oksanen *et al.*, 2013). Edaphic factors (H5) can also influence the distribution of herbivore species through their effects on plants. Soil pH is a main driver of vascular plant species richness in tundra (Gough *et al.*, 2000) and may thus drive the diversity of its primary consumers (Jetz *et al.*, 2009).

The role of biotic interactions (H6) at large spatial scales is increasingly recognized (Sandom *et al.*, 2013; Wisz *et al.*, 2013). Competition for resources and predation are the most investigated biotic interactions influencing species richness, and are equally able to promote or limit herbivore diversity (Chesson & Kuang, 2008). Plant productivity (H6a) is strongly correlated to herbivore biomass and diversity in terrestrial ecosystems (McNaughton *et al.*, 1989). However, more productive systems can sustain higher trophic levels that can control herbivore diversity (Oksanen *et al.*, 1981). In turn, predation (H6b) can increase herbivore species richness

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Table 1 Explanatory variables included in the models and underlying hypotheses that have been proposed to explain broad patterns of species richness at large spatial scales.

Hypothesis	Explanatory variables	Justification	Predictions
Energy			
Ambient energy	Mean annual temperature (H1a)	Physiological constraints limit species richness.[1] As mean annual temperature increases, climatic conditions are within the physiological tolerance range of more species, leading to greater species richness	Ambient energy variables at high latitudes will dominate species richness of herbivores over productive energy.[2] The effect of ambient energy at high latitudes might be stronger for mammals than birds, as shown at continental scales[3]
Productive energy	Normalized difference vegetation index (NDVI) (H1b)	Limits to species richness are set by the energy flowing through food webs; herbivore diversity is limited by net primary production of plants[4]	Correlates of net primary productivity may better represent the energy available to heterotrophs[2,5]
Environmental heterogeneity			
Habitat heterogeneity	Number of different habitat types (H2a)	Greater habitat diversity provides increased available niche space that can be used by a greater number of coexisting species[6]	Environmental heterogeneity is predicted to have a positive impact on species richness of herbivores,[7] probably more so in the case of non-migratory Arctic herbivores (i.e. most mammals). Topographic heterogeneity will increase local diversity of terrestrial vertebrates in the Arctic[8]
Topographic heterogeneity	Altitudinal range (i.e. difference between maximum and minimum elevation, H2b)	High rate of change in habitats along elevational gradients produces high between-habitat diversity in areas with greater topographic variability, increasing the potential for species coexistence[9]	
History/geography			
	Glaciation (H3)	More time since an area has been glaciated allows for colonization by more species and speciation[1]	We expect mammal species richness to be constrained by glaciation history. Birds (mostly migratory) are less likely to be affected by glaciation history
	Distance to coastline (H4)	In the Arctic distance to the coastline may play an important role in the functioning of ecosystems through the potential influence of productive marine ecosystems through subsidies on predators,[10] their lower topographic complexity and oceanicity	Coastal areas will host lower herbivore species richness.[1,9] This effect will be stronger for mammals, as many Arctic birds are wetland birds and may be positively associated with coastal areas
Edaphics	Soil pH (H5)	Soil pH is a main driver of vascular plant species richness in tundra[11]	Higher herbivore species richness is expected in less acidic substrates that host greater plant diversity. This effect will be stronger for birds than for mammals as has been shown at global scale[12]
Biotic interactions			
Plant–herbivore	Primary productivity (NDVI, H6a)	Primary productivity can determine the structure and abundance of herbivores and predators, increasing resource availability[13]	At a pan-Arctic scale more productive areas will host higher diversity of herbivores
Predator–herbivore	Predator species richness (H6b)	Species diversity of prey can increase as a result of predation, if predators reduce the strength of interspecific competition.[14] Alternatively, in simple food webs, predation can reduce species diversity via apparent competition[15]	Predator diversity can enhance the diversity of prey.[16] This effect might be related to diversity of body sizes[17] and we predict it will be stronger for mammalian herbivores, which represent a wider range of body sizes

Predictions for the role of each driver are indicated.

References: 1, Currie (1991); 2, Hawkins *et al.* (2003a); 3, Kissling *et al.* (2012); 4, Wright (1983); 5, Davies *et al.* (2007); 6, Kerr *et al.* (2001); 7, Stein *et al.* (2014); 8, CAFF (2013); 9, Kerr & Packer (1997); 10, Oksanen *et al.* (2013); 11, Gough *et al.* (2000); 12, Jetz *et al.* (2009); 13, Oksanen *et al.* (1981); 14, Paine (1966); 15, Holt (1977); 16, Ruifrok *et al.* (2015); 17, Legagneux *et al.* (2014).

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if it reduces interspecific competition (Paine, 1966) or reduce it if predators lead to apparent competition among prey (Holt, 1977). So far, the role of multi-trophic interactions in shaping broad-scale patterns of herbivore diversity across the Arctic has not been systematically evaluated.

The aim of this study is to identify patterns of herbivore diversity in the Arctic biome, and to relate these patterns to their potential drivers. Previous global-scale analyses of herbivores focused on specific taxonomic groups (birds, Kissling *et al.*, 2012; mammals, Sandom *et al.*, 2013) or explicitly excluded the Arctic region (Olff *et al.*, 2002). In this study, we focus on patterns of diversity of vertebrate herbivores (birds and mammals) as a cohesive guild with key functional roles in Arctic ecosystems. Further, we consider the Arctic as a unit; previous analyses of broad-scale diversity patterns merged the Arctic with temperate regions and consequently any patterns or drivers specific to the Arctic may have been masked by those observed in more diverse temperate areas. We reviewed the available data on vertebrate (birds and mammals) herbivore distribution at a pan-Arctic scale, and evaluated the applicability of the most relevant hypotheses that may explain patterns of species richness at regional scales to herbivores across the Arctic (Table 1). We analysed broad-scale patterns of herbivore species richness, and repeated the analysis separately for birds and mammalian herbivores. Overall we expected species richness of herbivores in the Arctic to be determined mainly by energy availability, either through temperature (H1a) or plant productivity (H1b). Biotic interactions (H6) with higher and lower trophic levels may also play a role in large-scale patterns of herbivore diversity (Wisz *et al.*, 2013). We predicted that herbivore diversity would be greater in areas with higher primary productivity but had no clear expectations with regard to predator diversity. We expected other drivers, such as environmental heterogeneity (H2), to play a secondary role in influencing the distributions of herbivores (Table 1). We expected different drivers of species richness for avian versus mammalian herbivores because of their different life histories and divergent adaptations. For instance, while most herbivorous birds in the Arctic are migratory, only some mammalian herbivores migrate seasonally (e.g. caribou/reindeer). Most mammals have other strategies to cope with the most limiting winter conditions, such as hibernation in some Subarctic mammals. Thus, the distribution and population dynamics of Arctic-breeding migratory birds might be more strongly influenced by processes occurring on their wintering grounds outside the Arctic (Ward *et al.*, 2005), while diversity patterns for mammalian herbivores might be more related to local conditions and historical influences (H3; Davies *et al.*, 2011) in the Arctic.

METHODS

Patterns of herbivore species and functional group richness in the Arctic

The analyses presented here are based on a database of distribution maps constructed for 73 extant vertebrate herbivore species occurring in the Arctic and Subarctic (CAFF, 2013). Only herbivorous species (excluding species that are predominantly frugivores and granivores) of birds (20 species) and mammals (53 species) were included (Table S2.1 in Appendix 2 in the Supporting Information). Distribution data for birds (Birdlife International & NatureServe, 2013) included species with breeding and non-breeding ranges in the Arctic; migratory pathways and vagrant species were excluded. For mammals, distributions of resident and migratory species were included (IUCN, 2013), as well as introduced and reintroduced species and domestic animals that graze in uncultivated land (such as sheep and semi-domestic reindeer). The original species distribution maps consisted of polygon layers that were rasterized to 100 km × 100 km grid cells to accommodate the resolution of the different information layers (see Appendix S1 for details on grain size), and were overlaid to calculate species richness for all herbivores, and separately for herbivorous birds and herbivorous mammals. Grid cells comprising more than 50% ice-covered land or water were excluded, resulting in 1227 cells for our analyses (Fig. S1.3 in Appendix S1).

To assess the extent of congruence in patterns of local species richness among subgroups of herbivores (birds, mammals) and between subgroups and overall herbivore diversity we calculated cross-correlations (Pearson correlations) between richness patterns (Kissling *et al.*, 2012).

Drivers of herbivore species richness in the Arctic

The explanatory variables considered in this study (Table 1) represent the main hypotheses that predict species richness patterns at large spatial scales. To assess the species–energy hypothesis we used mean annual temperature and the normalized difference vegetation index (NDVI) as measures of ambient (H1a) and productive energy (H1b), respectively. NDVI correlates strongly with net primary productivity and has been widely used as a productive energy metric (Evans *et al.*, 2005). In combination with energy, water availability has been well established as a driver of species richness at broad spatial scales (O'Brien, 2006), particularly for plants and at lower latitudes. At high latitudes, energy variables have a stronger effect on animal species richness (Hawkins *et al.*, 2003a), and therefore water-related variables were not included in the present study.

We evaluated the role of environmental heterogeneity by using proxies for habitat heterogeneity (number of land-cover types within an area, H2a) and topographic heterogeneity (range of elevation within an area, H2b). To account for historic and geographical factors we included a binary variable indicating whether an area had been glaciated since the LGM, approximately 21,000 years ago (H3; Currie, 1991; Davies *et al.*, 2007), and distance to coastline (H4; Currie, 1991; Kerr & Packer, 1997). Soil pH was included as a predictor to account for edaphic factors (H5). NDVI and species richness of predators of terrestrial vertebrate herbivores were used to account for biotic interactions (H6) with lower and

higher trophic levels, respectively. NDVI represents two non-exclusive hypotheses, productive energy (H1b) and biotic interactions with lower trophic levels (H6a), and can thus be interpreted from a strictly energetic point of view or as a proxy for plant–herbivore interactions. More details about how each explanatory variable was obtained is provided in Appendix S1.

Modelling approach

To evaluate the relative effects of these potential drivers of herbivore diversity in the Arctic, we built generalized least squares (GLS) models including species richness of all herbivores, herbivorous birds and herbivorous mammals as response variables. The initial (full) models included the eight explanatory variables presented above as additive factors (Table 1): mean annual temperature (H1a), NDVI (H1b and H6a), habitat heterogeneity (H2a), topographic heterogeneity (H2b), glaciation history (H3), distance to the coast (H4), soil pH (H5) and predator species richness (H6b). Available raw data for each of the candidate explanatory variables were rescaled to the same grid as the species richness data (for details on sources, raw resolutions and values, and treatment of explanatory variables see Appendix S1).

Univariate relationships between each explanatory variable and the responses were visually inspected for linearity (Appendix S1). We tested for collinearity and multicollinearity among explanatory variables, using pairwise linear correlations and variance inflation factors (VIFs). Predator species richness was correlated with NDVI ($r = 0.56$); therefore, to assess the relationship between predator species richness and herbivore richness, independent of NDVI, we took the residuals of the regression predator richness–NDVI and included them in the models. This approach assigns priority to one of the variables over the shared contribution, assuming that one variable is functionally more important than the other (Graham, 2003). We checked the implications of this assumption by rerunning the models with the residuals of the regression NDVI–predator richness. Results were essentially the same (Appendix S3); therefore, the results presented here are from the first approach. Mean annual temperature was correlated to NDVI ($r = 0.42$) and soil pH ($r = -0.42$). Inclusion of mean annual temperature and NDVI in the models suggested collinearity problems in the model averaging process (see below). As these variables represent different aspects of the species–energy hypothesis and we were interested in assessing the relative role of each, we followed the same procedure as above to statistically separate their effects, taking the residuals of the regression NDVI–mean temperature. All other pairwise correlations had $r < 0.4$, and VIF values for the explanatory variables were <1.6 in all cases. This approach allowed us to test the direct, independent effects of the explanatory variables. All explanatory variables were standardized before including them in the models, so that estimates of coefficients are directly comparable.

Spatial autocorrelation can bias estimates of environmental parameters, and is of particular concern in analyses of geographical patterns of species richness when using regression models that assume independence of observations (Davies *et al.*, 2007). GLS models are well suited to deal with spatially structured data because they can incorporate spatial covariance structures within the models to control for spatial autocorrelation. We fitted exponential variance–covariance structures where *x*- and *y*-coordinates of pixel centroids were included as spatial variables. Exponential structures were the best-fit choice among spatial covariance structures, and including them in the models effectively removed spatial autocorrelation in the residuals (Appendix S1).

Our eight explanatory variables represent non-exclusive hypotheses that have been proposed to explain species richness patterns. We therefore built GLS models for all possible combinations of the eight explanatory variables (256 models for each of the three response variables) and used a model averaging approach based on the Akaike information criterion (AIC) to assess the relative importance of these variables. Estimated coefficients of each variable were then averaged across all models in which they were present and weighted according to the probability associated with each model (see Table S1.2 in Appendix S1 for the top-ranking models, with $\Delta AIC < 2$). Modelling assumptions, including the lack of independence due to spatial autocorrelation, were checked by visually inspecting residual patterns of the full models. All statistical analyses were conducted in R 3.1.2 (R Development Core Team, 2014), using the libraries '~~AICcmodavg~~' and 'nlme' (see Appendix S1).

Alternative methods of analysis, such as structural equation modelling, have been used in macroecological studies to assess direct and indirect effects of different drivers of broad-scale biodiversity patterns (e.g. Kissling *et al.*, 2008; Sandom *et al.*, 2013). However, these techniques cannot deal efficiently with spatial autocorrelation (e.g. coefficient shifts when comparing spatial and non-spatial models; Bini *et al.*, 2009) and in the presence of such effects (as in our study; see Appendix S4) they can yield biased results. Our multiple regression approach using the residuals of collinear variables allowed us to focus on the direct effects of explanatory variables while accounting for spatial autocorrelation.

RESULTS

Patterns of herbivore species richness in the Arctic

Local species richness of vertebrate herbivores in the Arctic was low and ranged between 1 and 23 species (median 14), with peaks in diversity observed in Subarctic western North America (Fig. 1a; Appendix S5). Mammalian herbivores represent 72.6% of vertebrate herbivore species in the Arctic and their species richness ranged between 0 and 19 (median 8). Species richness of mammalian herbivores also peaked in Subarctic western North America, although over a more restricted range than overall herbivore richness; mainly in eastern Beringia (Fig. 1c). Species richness of herbivorous

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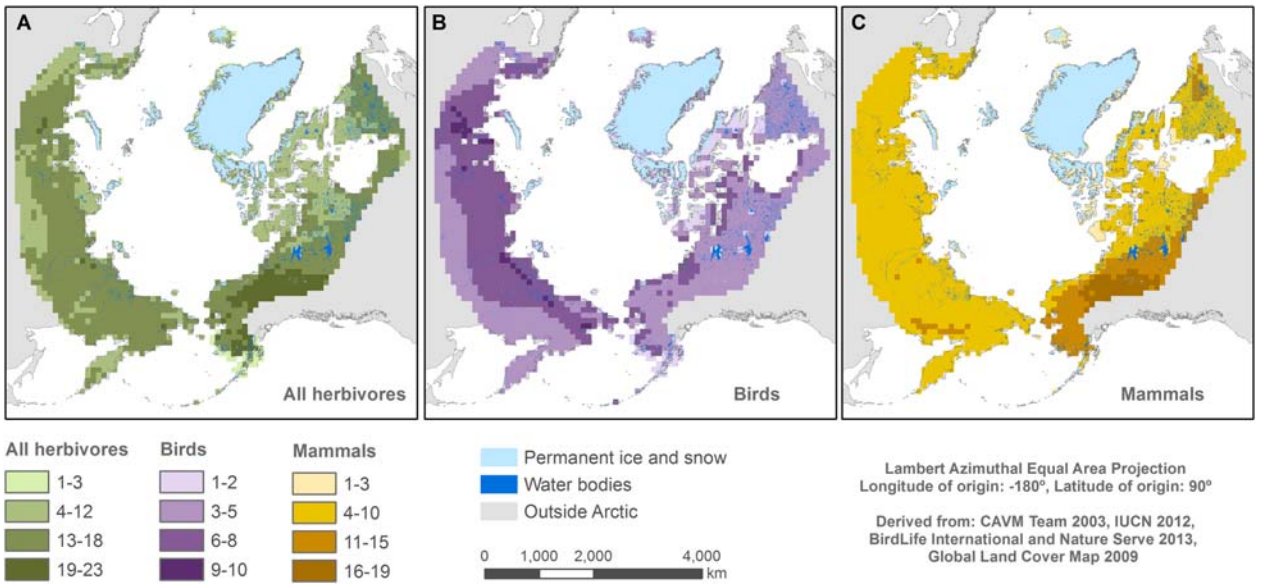

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Figure 1 Distribution maps of species richness of (a) all herbivores, (b) herbivorous birds, and (c) herbivorous mammals. Grid cells are 100 km × 100 km in size.

birds ranged between 1 and 10 species (median 5) and was highest in Eurasia, around the Ob River, and in the Siberian Low Arctic east of the Lena River (Fig. 1b).

The richness of mammalian herbivores showed the highest congruence ($r = 0.87$) with overall herbivore species richness, while the richness of birds overlapped little with overall herbivore richness ($r = 0.40$). Species richness of birds did not overlap with that of mammalian herbivores ($r = -0.11$; Fig. S1.6 in Appendix S1).

Drivers of herbivore species richness in the Arctic

Based on the associated Akaike weights, no single model had strong support, further justifying the use of model averaging procedures. For instance, the cumulative Akaike weight for models with $\Delta AIC < 2$ (Table S1.2 in Appendix S1) was 0.45 in the case of all herbivores, 0.50 for birds and 0.53 for mammals. The 95% credibility sets, i.e. the set of models that include the best approximating model with 95% confidence (cumulative Akaike weight 0.95), included 41 models in the case of all herbivores, 32 for birds and 50 for mammals. Variable importance scores consistently showed NDVI and predator species richness to be the most important variables across herbivore groups (Fig. 2). Mean temperature was more important in the models for all herbivores than those for birds and mammals, while distance to the coast was important in avian and mammalian models but not in the model including all herbivores.

Patterns of herbivore species richness in the Arctic were consistently and positively correlated with NDVI (H1a and H6a) and with species richness of predators (H6b); other explanatory variables had minimal effects or affected only some subgroups of herbivores (Fig. 3). Overall species richness of herbivores was greater in warmer areas with higher NDVI and with more species of predators (Figs 3 & 4). Similar patterns were observed in our separate analyses of herbivorous birds and mammals. Correlations with NDVI and predator species richness were stronger for mammalian herbivores than for birds (Fig. 4b,c). Interestingly, we found contrasting effects for avian and mammalian herbivores for the only other explanatory variable that affected richness, namely distance to the coast (H4). Mammalian species richness was positively associated with areas further from the coast, whereas avian species richness was maximized closer to the coast (negative effect). Glaciation history (H3) did not have a significant effect on species richness of herbivores, but mammalian herbivores tended to be more diverse in areas that had not been glaciated since the LGM (95% CI = [–0.258, 0.033]). Environmental heterogeneity (topographic or habitat, H2) and soil pH (H5) had no effect for any of the groups of herbivores considered.

DISCUSSION

Our analysis of overall patterns of herbivore species richness represents the first attempt to identify the drivers of diversity of a main trophic group across the Arctic biome. We found strong support for the species–energy hypothesis (productive energy) and for the role of biotic interactions in shaping herbivore diversity at a pan-Arctic scale, with greater herbivore species richness in areas presenting the highest NDVI and predator richness.

As predicted, overall richness of herbivore species in the Arctic was highest in Subarctic regions, with higher values of the energy-related variables. We detected a positive effect of mean annual temperature on species richness of all herbivores, but this effect was much weaker than that of productive energy, even when the effects of both variables were

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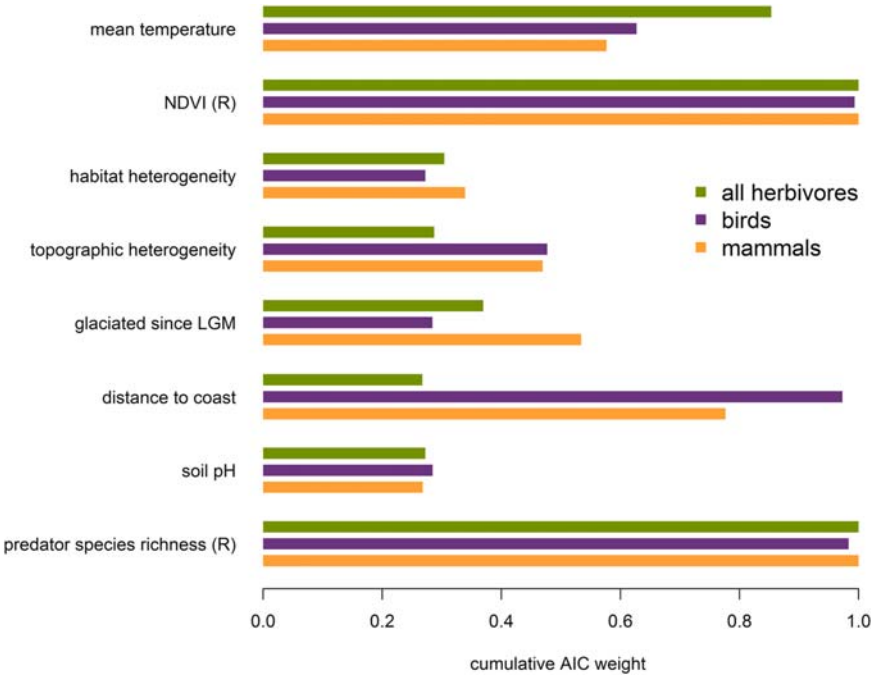
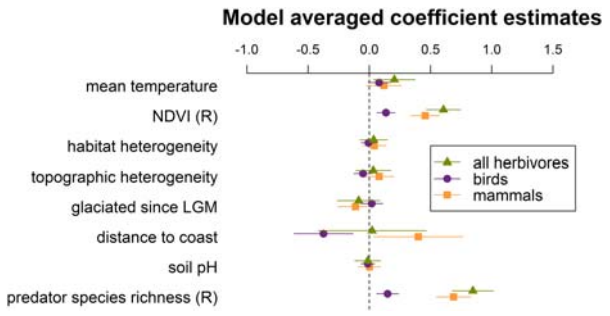


Figure 2 Variable importance scores for all herbivores (green), herbivorous birds (purple) and herbivorous mammals (orange). The relative importance of each variable is calculated summing the Akaike weights for all models in which that variable appears. Variable weight can be interpreted as the probability of that variable being a component of the best model, and can be used to rank the predictors in order of importance. NDVI, normalized difference vegetation index; LGM, Last Glacial Maximum.

statistically separated. Productive energy metrics, such as NDVI, integrate the variables that constrain the conversion of energy to plant biomass, i.e. water and nutrient availability, temperature and light; as a composite variable, NDVI would have greater explanatory power than that of mean annual temperature alone. An alternative explanation for the weak correlation between mean annual temperature and herbivore diversity is that other aspects of ambient energy, such as the temperature during the different seasons, are more relevant in the highly seasonal Arctic environments. Further, NDVI represents both the species–energy hypothesis (productive energy, H1b) and the role of biotic interactions (H6a). NDVI has been successfully used as a predictor of phytomass in the Arctic (Epstein *et al.*, 2012) and to study interactions between herbivores and plants (Olofsson *et al.*, 2012; Doiron *et al.*, 2015). These hypotheses may thus be seen as two sides of the same coin, where the specific mechanisms driving the positive correlation between primary productivity and herbivore diversity cannot be separated (Evans *et al.*, 2005).



COLOR

Figure 3 Model averaged coefficients for drivers of species richness of all herbivores (green), herbivorous birds (purple) and herbivorous mammals (orange). All predictors were standardized, so coefficients are directly comparable. Coefficients were averaged across all models, and means and 95% CI are shown. Coefficients different from zero (i.e. not overlapping the vertical dashed line) had a significant effect on species richness of herbivores. NDVI (R): effect of normalized difference vegetation index (NDVI) independent of mean annual temperature. Predator species richness (R): effect of predator species richness independent of NDVI. LGM, Last Glacial Maximum.

In our study, predator diversity was also related to patterns of herbivore diversity (Chesson & Kuang, 2008), with consistently higher herbivore species richness in areas with higher predator species richness. The effect of biotic interactions on species distributions has been generally assumed to prevail at a local scale, and its relevance at regional or global scales has been neglected until recently (Wisz *et al.*, 2013; Belmaker *et al.*, 2015). Diversity in adjacent trophic levels can be positively correlated simply because both trophic levels respond to the same environmental factors in a similar way (Hawkins & Porter, 2003). This is not the sole explanation for the correlation between herbivore and predator diversity in the Arctic, since the positive association between species richness of herbivores and predators was evident even when the effect of NDVI on predator richness was statistically removed. The greater variety of hunting strategies in a diverse predator community can favour increases in prey species richness, as it provides opportunities for niche differentiation in anti-predator strategies of prey (Ruifrok *et al.*, 2015). An alternative, non-exclusive explanation is that increased herbivore diversity is driving predator species richness. Predator and prey species richness can be strongly associated at broad spatial scales, even when the effects of other environmental

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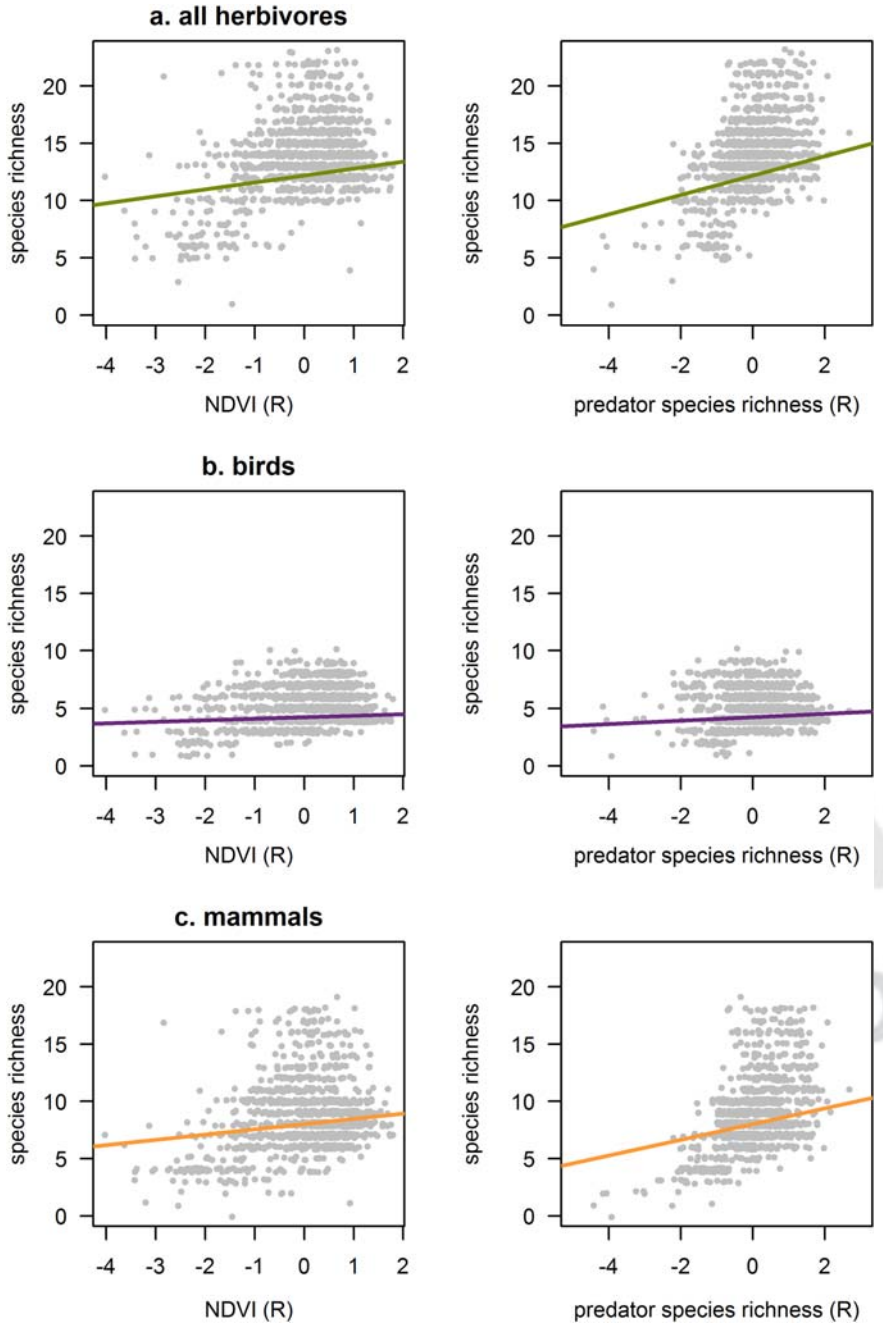

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Figure 4 Predicted relationship between species richness of (a) all herbivores, (b) herbivorous birds, and (c) herbivorous mammals in the Arctic, and plant productivity (normalized difference vegetation index, NDVI; standardized residuals; left) and species richness of predators (standardized residuals; right) based on the multi-model average. Fitted lines for the partial effects (with all other predictor variables set to their means) are shown; points indicate observed values with random noise added to improve visualization.

drivers are taken into account (Sandom *et al.*, 2013). Bottom-up (prey-to-predator) effects seem to be stronger than top-down predator forces at a global scale (Sandom *et al.*, 2013), but the strength of bottom-up and top-down control of herbivore populations may also depend on primary productivity (Oksanen *et al.*, 1981; Legagneux *et al.*, 2014).

When analysed separately, species richness of avian and mammalian herbivores showed contrasting patterns with respect to distance to the coast. Higher values of mammalian species richness were associated with areas farther from the coast, while greater numbers of bird species were associated with coastal areas. These patterns were not evident for the overall richness of herbivores, probably because the influence of distance to the coast on each group of herbivores more or less cancelled out. At continental scales in North America, higher species diversities of birds and mammals are found in inland locations (Currie, 1991; Kerr & Packer, 1997). However, higher avian species richness in coastal areas in the Arctic is probably related to the predominance of wetland birds among Arctic herbivores. Tundra swans and geese (13 of the 20 bird species analysed) tend to congregate in lowland coastal areas during breeding and moulting periods and their summer distribution may respond to specific requirements for breeding (Ward *et al.*, 2005). The cooling effect along the coastline or less complex topographic landscapes in coastal

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areas may be other factors involved. Additionally, coastal locations in the Arctic provide subsidies to predators from marine ecosystems that can then maintain more abundant populations (Gauthier *et al.*, 2011; Therrien *et al.*, 2014).

Glaciation history, environmental heterogeneity and edaphic conditions (soil pH) had no detectable effect on the observed patterns of herbivore richness. In the case of glaciation history, there was a non-significant trend towards higher diversity of mammals in areas that remained ice-free. The fact that we did not detect a strong signal of glaciation history might also be related to the coarse resolution of our grid cells (100 km × 100 km), since studies presenting strong support for the role of glaciation history have been conducted at finer spatial scales (e.g. Normand *et al.*, 2013). Current distribution patterns of terrestrial mammals in the Arctic are linked to the distribution of refugia that remained ice-free during the LGM, and may reflect patterns of colonization into newly forming tundra habitats as ice retreated during the Holocene (Waltari & Cook, 2005). Historical influences on broad-scale species richness patterns might be masked by present-day environmental drivers and fine-scale analyses would be needed to resolve their influence (Hawkins *et al.*, 2003b). Moreover, most herbivorous birds in the Arctic are migratory, so they may be less constrained by glacial history of an area as they may more easily colonize newly deglaciated areas.

Our results suggest the importance of considering adjacent trophic levels when investigating patterns of herbivore species richness in the Arctic and the complex nature of plant–herbivore–predator interactions. The need to include biotic interactions and food-web approaches to study the functioning of changing tundra ecosystems has been recently highlighted (Gauthier *et al.*, 2011; Legagneux *et al.*, 2014). The inclusion of abundance data for herbivore populations would increase our understanding of the relative importance of productivity and predator–prey interactions as drivers of species diversity through food webs, but reliable information is only available for some species (CAFF, 2013). Furthermore, high-quality data on the distribution of herbivores at finer temporal and spatial scales will be needed to further understand the drivers of herbivore diversity in the Arctic. For example, range maps represent species distribution without a temporal reference, which might limit our ability to detect environmental correlates of species richness if species are shifting ranges, as predicted under ongoing global change or, at a finer temporal resolution, for migratory species. It must be kept in mind that, given the coarse spatial resolution of the data available, discarding pixels that encompassed more than 50% ice-covered land in 100 km × 100 km pixels results in the loss of information from many High Arctic islands (e.g. Svalbard or many islands of the Canadian Arctic Archipelago). Ice- and snow-covered land can serve as an important habitat for a number of species of mammals and birds (Rosvold, 2016). Rather than implying that these areas could not function as hotspots of herbivore diversity, this points to the need to develop remote-sensing products and species distribution maps with a resolution better tailored to the spatial attributes of Arctic ecosystems. Despite their limitations, such large-scale approaches are particularly needed for the Arctic, where the land area is vast, covering more than 15,000,000 km^2 of terrain that is often difficult to access. Regional-scale indices or maps of herbivore diversity based on remote-sensing data (e.g. NDVI or interpolated temperature data) may inform conservation priorities (e.g. the WWF RACER project; http://wwf.panda.org/what_we_do/where_we_work/arctic/what_we_do/climate/racer/) or guide research efforts in the Arctic.

It is important to understand current broad-scale patterns of diversity in Arctic ecosystems so that future changes under climate warming can be detected. Our approach focusing solely on the Arctic allowed us to uncover patterns that are specific to this region and that had not been detected in previous studies. For example, we found that the diversity of herbivorous birds was higher in coastal areas, a pattern that contrasts with what has been found at broader continental scales (i.e. higher bird diversity inland; Currie, 1991). These patterns were not evident in previous studies including all biomes because global patterns are largely driven by regions with higher diversity. This knowledge will also help identify diversity 'hotspots' that can be protected in the face of increasing commercial activity in the north. Our finding that coastal regions are centres of diversity for birds highlights the importance of identifying critical areas for protection before these areas are developed for oil and gas, transport and other human activities. Recent changes in vertebrate herbivore populations in the Arctic are mostly related to local increases in abundance (CAFF, 2013), but also to shifts in distribution (Gilg *et al.*, 2012). Over the long term, the abundance of certain herbivores may increase, but Arctic specialist species may be gradually replaced by range-expanding species from the south. Such changes are likely to alter the interactions among herbivores that determine the structure of their communities and, ultimately, the impacts that herbivores have on tundra vegetation.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

AQ2

Appendix S1 Extended methods.
Appendix S2 List of species.
Appendix S3 Extended results.
Appendix S4 Results of structural equation models.
Appendix S5 kmz file for the maps of herbivore richness.

BIOSKETCH

The research team is part of the Herbivory Network (http://herbivory.biology.ualberta.ca). The aim of this international research network is to investigate the role of herbivores in arctic and alpine ecosystems. The network comprises more than 100 members from different countries and at different stages of their research careers, from graduate and undergraduate students to well-established scientists. In several ongoing projects, the Herbivory Network uses different approaches, including meta-analytical, experimental and observational studies, to unveil the role of herbivory in northern and alpine ecosystems. A large part of the current activity of the Herbivory Network is focused on developing standardized protocols that will enable multi-site comparisons and coordinated experiments.

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